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STUDY ON THE SEGMENTATION OF THE HEAD OF INSECTS, BASED UPON COMPARISONS AS OUTLINED IN COMSTOCK AND KOCHI, "THE SKELETON OF THE HEAD OF INSECTS," . . . . *Ruby C. Hosford.*

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THE KANSAS UNIVERSITY SCIENCE BULLETIN.

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Segmentation of the Head of Insects.

Plates I to IV.

BY RUBY C. HOSFORD.

THE question of the segmentation of the head of insects has been much discussed, with the result that different observers have recognized from one to seven segments therein.

Savigny (1816) made a very important step toward the solution of the problem by suggesting that the movable appendages of the head were homodynamous with legs. Comparative anatomists, then, accepting this and seeing that each segment in the body of an insect has only one pair of appendages, have concluded that there are at least four segments in the head: *i. e.*, the antennal, the mandibular, the maxillary, and the second maxillary or labial. They also suggest that since the eyes in certain crustacea are borne on movable stalks, they may be the appendages of a fifth segment.

From this point the embryologist carries on the study. He has found that in the embryo there exist distinct segments, each corresponding to a pair of mouth parts. It has also been found that in some stages of development there are at least three pairs of distinct ganglia which go to make up the subœsophageal ganglion. Each of these pairs of ganglia corresponds to a pair of mouth parts.

Wheeler ('93) observed rudimentary intercalary or premandibular appendages, which others have homologized with the crustacean second antennæ. Folsom has found rudimen-

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tary chitinized intercalary appendages in adults of *Tomocerus, Orchesella,* and other Collembola.

Folsom in his study of the embryo of *Anurida* found seven pairs of primary ganglia, the extra one being the fifth, between those of the mandibular and maxillary segments. This is called the superlingual segment. According, then, to the conclusions set forth from the study of comparative anatomy and embryology, the insect head is composed of seven segments: the *antennal,* the *mandibular,* the *maxillary,* the *second maxillary* or *labial,* the *premandibular* or *intercalary,* the *ocular,* and the *superlingual.*

The order of arrangement of these segments may be determined by the position of the primitive ganglia that innervates them.

The supraœsophageal ganglion, or the brain, is composed of three pairs of primary ganglia: the protocerebrum innervates the compound eyes and the ocelli or the ocular segment; the deutocerebrum, the antennæ or antennal segment; and the tritocerebrum, the labrum or premandibular segment. The subœsophageal ganglion is composed of four pairs of primary ganglia: the first innervates the mandibles or mandibular segment; the second, the superlinguæ or superlingual segment; the third, the maxillæ or maxillary segment; and the fourth, the labium or second maxillary segment.

We have, then, the following order:

1.—Ocular.
2.—Antennal.
3.—Intercalary.
4.—Mandibular.
5.—Superlingual.
6.—Maxillary.
7.—Labial.

Having now decided that there are seven segments united to form the head capsule of insects, we wish to determine what sclerites belong to the different segments. Using the work of Comstock and Kochi as a working outline, I have endeavored by a series of comparisons to form for myself an opinion on at least some of the following points:

Areas of the external skeleton of the head; the structure of a typical segment; and the sclerites belonging to each head segment.

I. Areas of the External Skeleton of the Head.

By making a comparative study of the following insects: Orthoptera—cricket, cockroach, *Corydalis* (larva and adult), walking-stick, mantis, *Dahinia, Orchelimum, Decticinæ,* and grasshopper; and Coleoptera—*Amblychila,* I have made the following observations:

1. (*E. SU.*) *The Epicranial Suture,* though indistinct and small in *Dahinia, Orchelimum,* and *Decticinæ,* is present in all of the Orthoptera and can easily be traced in the *Amblychila.*

2. (*F.*) *The Front,* the first single sclerite between the arms of the inverted Y (*E. SU.*), is always present. It is enlarged by pushing up of *E. SU.;* smallest in larva of *Corydalis.* In the orthopterous forms it includes the paired ocelli and median ocellus when present. The beetle studied has no ocelli.

3. (*Cl.*) *The Clypeus,* the second of the single sclerites between *E. SU.* and the mouth, is sometimes separated from *F.* by a deep suture, and sometimes seems but a continuation of it, the suture being absent. The point of separation between the two is always to be determined by the invaginations of the anterior arms of the tentorium.

The clypeus is often divided by a transverse suture into *clypeus first* and *clypeus second.*

The clypeus is really composed of three parts in a transverse row, the part on the median line being *C. proper,* the lateral ones on the frontal margin being *Antecoxal pieces* of the mandibles. This division is shown especially well in the larva of the *Corydalis.* They can be located in the other specimens merely by their assumed position.

4. (*L.*) *The Labrum,* upper lip of the mouth, last single sclerite between *E. SU.* and the mouth, often appears as an appendage, but is really a portion of one of the head segments. In some cases the markings make it appear as composed of two parts.

5. (*E.*) The *Epicranium* in the forms studied includes the paired sclerites of the skull. These sclerites constitute the sides of the head and that part of the dorsal surface that is behind the arms of the epicranial suture (*E. SU.*).

6. (*V.*) *The Vertex,* the first pair of paired sclerites behind the arms of *E. SU.,* the dorsal portion of the epicranium; or that portion which is next the front and between the com-

pound eyes. In the heads of *Orchelimum, Decticinæ* and grasshopper these sclerites are much smaller than in the other specimens studied. The smaller the frontal sclerite the larger the vertex.

7. (*O.*) *The Occiput,* the part of the head behind the vertex and surrounding the occipital foramen. This is not always a distinct sclerite, but when it is, as in the *Corydalis,* it appears to be formed from the tergal portion of the united postgenæ. This is present in the grasshopper, *Corydalis* and *Amblychila.*

8. (*G.*) *The Genæ,* the lateral portions of the epicranium just back of and below the compound eyes.

9. (*P. G.*) *The Postgenæ.* Each genæ was divided by a more or less well-marked suture, and the part back of this forms the *postgenæ.* Comstock thinks that it is the upper part or continuation of these that forms the occiput. Packard thinks the postgenæ are distinct from the occiput, which he considers as a part of the labial segment. I favor Comstock's view, for, in the grasshopper especially, the occiput seems so evidently a continuation of the postgenæ.

10. (*Gu.*) *The Gula,* which is often absent, when present forms the ventral wall of the hind part of the head, and bears the labium or second maxillæ.

11. *The Cervical Sclerites,* the sclerites of the neck. Of these there are dorsal, ventral, and lateral ones.

There are two dorsal cervical sclerites in the neck of the cockroach. In *Amblychila* I distinguished none.

Melanoplus has two lateral cervical sclerites on each side. Between these is a prominent apodeme. I also found what appeared to be a smaller apodeme on each side. In *Amblychila* there are two small chitinized spots, one on each side, which are probably vestiges of the lateral cervical sclerites.

In the cockroach there are two ventral cervical sclerites; in the cricket there are five, arranged in two series; in *Stenopelmatus* there are three, arranged in two series; in *Corydalis* and *Amblychila* these sclerites are not found, but the gula is present.

Snodgrass thinks that these cervical sclerites do not belong to the head, but to thorax. He designates them as the *microthorax.*

12. (*OS.*) *The Ocular Sclerite.* "Each compound eye is situated in the axis of an annular sclerite which may be the basal segment of the ocular appendages." These annular sclerites are the ocular sclerites. They show especially well in the cricket and *Amblychila.*

13. (*AS.*) *The Antennal Sclerites,* annular sclerites at the base of each antenna.

14. (*Tr.*) *The Trochantin of the Mandible,* a distinct sclerite between the mandible and the genæ in some insects; indeed, in all that I studied.

II. The Structure of a Typical Segment.

Since the abdominal segments have lost their appendages, it is evident that a reduction of certain parts has taken place there, which makes it impossible to use them as typical segments. The thoracic segments are the more typical.

The parts of a thoracic segment as generally recognized are as follows: a ventral part, sternite; two lateral parts, pleurites; and a dorsal part, tergite. Each segment is composed of two subsegments. "The line separating the subsegments passes, on the pleural aspect, between the episternum and the epimeron; and, on the tergal aspect, between the scutum and scutellum"; on the sternal aspect, between the sternum and sternellum.

The line of union between the episternum and epimeron is the apodeme, which is an invagination of the body wall. The division on the sternal aspect of most insects is not easily recognized, but it shows plainly on the metathorax of *Stenopelmatus* and the nymph of *Pteronarcys.* As the apodemes show the division of the pleural subsegments, so the furca shows their division on the sternite.

Embryologists have also proven that each segment "is composed of a median and two lateral fields, and that the appendages are developed as evaginations of the lateral fields."

III. Sclerites Belonging to Each Head Segment.

1. *Ocular or Protocerebral.*

Tergal sclerites. No trace.

Sternal sclerites. Front. Contains ocelli which are innervated by protocerebrum. Decided ridge in *Mantis* front may indicate sternum and sternellum.

Pleural sclerites.—One-half of vertex and corresponding gena. These probably represent lateral elements of sternum, because they enclose the ocular sclerite, which represents the appendage of this segment.

Appendages. Ocular sclerite.

2. Deutocerebral or Antennal.

Tergal sclerites.—No trace.

Sternal sclerites.—Clypeus. Formed from portion of procephalon, the central swelling of the cephalic end of the body of embryo insects. It is not the first segment nor does it contain the mouth, which falls in the tritocerebral segment, but is between the front and the mouth; therefore, it is a sclerite of the second segment.

Pleural sclerites.—Antennal sclerites. Lateral elements of sternite, because the antennæ arise from them. Even when antennæ seem to be postoral the basal part of the rudiment of the antennal sclerite appears to abutt against the procephalon.

Appendages.—Antennæ.

3. Tritocerebral or Second Antennal.

Tergal sclerites.—No traces.

Sternal sclerites.—Labrum. Formed from procephalon; contains mouth, which is in third segment.

Pleural sclerites.—None determined.

Appendages.—Second antennæ, when found.

4. Mandibular.

Tergal sclerites.—Occiput. Continuation of the postgenæ which form the pleural sclerites. Packard considers this as belonging to the sixth or labial segment, but as far as my observations have gone I agree with Comstock. It seems to me to be a continuation of the postgenæ, which Packard also considers as belonging to the mandibular segment.

Sternal sclerites.—Pharyngeal sclerites. Found in the floor of the mouth cavity of *Melanoplus* on each side just behind the superlinguæ. They are back of the superlinguæ, which shows that they must precede superlingual sclerites in the course of the invagination of the mouth. They are also closely connected with the mandible. Since in this region sclerites are frequently developed secondarily, Comstock does not think

that much stress should be laid on this supposed homology. I, myself, do not think the evidence brought forward on this point is very conclusive.

Pleural sclerites.—Postgenæ. A suture which is the more or less open mouth of an apodeme divides the postgenæ as does the apodeme the pleurites of the thoracic segments. The mandibles, like the coxæ of the legs, fit into the openings where the apodemes begin.

The antecoxal pieces. In *Gryllus* and the larvæ of *Corydalis* the mandibles articulate with a sclerite distinct from the clypeus. This corresponds to the antecoxal piece in the thoracic segments.

Appendages.—Mandible and trochantin, a small sclerite at base of mandible in Orthoptera and *Amblychila.*

5. *Superlingual.*

Tergal sclerites.—None found.

Sternal sclerites.—Represented by that part of the floor of the mouth cavity which bears the superlinguæ.

Pleural sclerites.—Represented by that part of the floor of the mouth cavity which bears the superlinguæ.

Appendages.—Superlinguæ.

6. *Maxillary.*

Tergal sclerites.—None found.

Sternal sclerites.—Lingua. This is the unpaired portion of the hypopharynx, and evidently pertains to the sternite of this segment, because it arises between the rudiments of the maxillæ.

Pleural sclerites.—Maxillary pleurites. There is a narrow band or sclerite that runs around the posterior margin of the epicranium. This is the posterior pleurite. The anterior one is scarcely visible except in a few insects, as in the cockroach and cricket. Between these two sclerites is an apodeme, which forms the posterior arm of the tentorium. In *Amblychila* this apodeme and the two sclerites are very clearly seen.

Appendages.—Maxillæ.

7. *Labial or Second Maxillary.*

Tergal sclerites.—Probably dorsal cervical sclerites.

Sternal sclerites.—Ventral cervical sclerites and gula. The ventral sclerites are often arranged in two series, showing the subsegments, and divided into two or three in each segment, showing the lateral and median fields. In some insects, as adult of *Corydalis* and *Amblychila,* they have united to form the gula.

Pleural sclerites.—Lateral cervical sclerites. These sclerites are best shown in *Melanoplus.* These under high-power lenses showed one prominent apodeme and one smaller one. Comstock mentions but one apodeme, and thinks that it helps to prove that these are the epimeron and episternum of a segment. The posterior of these sclerites articulates with the episternum of the prothorax, and the anterior one with what we believe to be the epimeron of the maxillary segment. I do not know what the smaller apodeme signifies.

Appendages.—Second maxillæ or labium.

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